

Personality and density affect nest defence and nest survival in the great tit

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Abstract Recent studies suggest that individual variation in behaviour of prey individuals may cause distinctive responses to nest predators and cooperation with conspecifics. We assessed individual differences during a novel object test and whether these responses were related to nest failure and survival of females during incubation. We additionally carried out experimental trials in natural field conditions using a stuffed pine marten, a principal nest predator, to test for a relationship between neophobia and mobbing predators. Our results show that antipredator responses of breeding great tits are dependent on their personality and personality type of neighbouring conspecifics. We found that neophilic individuals (those that rapidly resumed feeding of nestlings in the presence of a novel object) have an advantage over neophobic individuals (those that slowly resumed feeding of nestlings in the presence of a novel object) in their reproductive success, as measured in numbers of successful nests and of females that survived. Furthermore, neophilic-neophilic pairs exhibited stronger antipredator mobbing responses than neophobic-

neophobic pairs. Results show that consistent individual differences in response against novel objects and antipredator behaviour are related, and that these responses are important predictors of nest failure in breeding great tits.

Keywords Nest defence · Mobbing behaviour · Breeding success · Novel object · Neophobia · Great tit · *Parus major*

Introduction

Nest predation is the primary cause of reproductive failure for most birds and, thus, represents an important source of natural selection (Ricklefs 1969; Martin 1995). Recent advances in the theory of avian life history have shown that nest predation may play a key role in the expression of avian reproductive strategies (Fontaine and Martin 2006). Furthermore, empirical studies indicate that adult birds can assess the levels of nest predation risk and alter their antipredator behaviour (Krama et al. 2012a; Seppänen et al. 2011; Fontaine and Martin 2006) and reproductive strategies (Wiklund and Andersson 1980; Mönkkönen et al. 2009; Thomson et al. 2011).

The nests of woodland passerine birds are usually well spaced, and concealed by their positioning and cryptic structure, characteristics that should reduce nest predation (Lack 1968). Furthermore, clumped distribution of breeding birds and nest sites is known to occur in some species and may bring benefits in terms of improved reproductive success. The idea that individuals prefer to settle closely to conspecific individuals, at least in some species, can be traced back many decades (Lack 1948; Svårdson 1949; Kalela 1952; Wiklund and Andersson 1980; Krams and Krama 2002). Stamps (1988) suggested that aggregated distribution may provide improved ability to defend against intruders or competitors and provide protection against predators by means of communal defence.

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Thus, costs of communal nesting may be traded off against increased fitness under predation risk.

Mobbing of predators is one behaviour pattern that is common among social groups of passerines and that may be especially effective among clumped breeding species. Mobbing involves an attack on a predator by prey individuals to drive it away and is a widespread behaviour among vertebrates (Curio 1978; Flasskamp 1994; Griesser 2009; Templeton et al. 2005; Berzins et al. 2010; Krams et al. 2010; Lima 2009; Cheney et al. 2011; Davies and Welbergen 2009; Welbergen and Davies 2009). The more individuals that participate in a mob, the higher the chance of deterring the predator (Robinson 1985; Verbeek 1985; Picman et al. 1988; Pavey and Smyth 1998; Krams et al. 2009; Krama et al. 2012a). This might explain the proclivity of even territorial birds such as pied flycatchers and great tits to nest near one another (Grabowska-Zhang et al. 2012a, b; Krams et al. 2006b, 2008, 2010).

Reduction of predation risk through direct defence by group members has been suggested to be a significant benefit of group living (Krause and Ruxton 2002). In some species, all group members are assumed to share defence duties equally (Elgar 1989; Caro 2005). However, several studies have shown variation in defence behaviour among group members (Krams and Krama 2002; Arlet and Isbell 2009; Carter et al. 2009; Krams et al. 2009). Those individuals with neighbours that vigorously defend against predators may experience decreased predation risk even without participating in defence activities, and to therefore avoid energy loss and injuries associated with defence efforts (Dugatkin and Godin 1992; Stenhouse et al. 2005; Kazama and Watanuki 2010).

The observed differences in defence against predators may be explained by individual variation in their behavioural type related to heritable temperament or personality traits, which represent a complex of correlated, heritable behavioural traits consistent across contexts (Groothuis and Carere 2005; Sih and Bell 2008; Dingemanse and Wolf 2010; Schuett et al. 2010; Aplin et al. 2013). Major axes of personality variation are exploratory behaviour (e.g. Verbeek et al. 1994; Carere et al. 2005), activity (e.g. Sih et al. 1992), aggression (e.g. Carere et al. 2005; Huntingford 1976), sociality (Cote and Clobert 2007), risk taking and neophobia (e.g. Greenberg 1983). It is known that individual birds differ in the way they respond to a novel object and, at the extremes of the variation, may be assessed as 'neophobic' or 'neophilic' individuals (Greenberg 1983; Mettke-Hofmann et al. 2009; Herborn et al. 2010). The ecological significance of neophobia is considered as a measure of propensity to approach and learn about new feeding opportunities and it may also be a measure of response to stressors in general (Groothuis and Carere 2005; Richard et al. 2008). Consequently, it could be expected that neophobia may cause differences in individual reactions

to nest predators and affect dominance interactions and cooperation with conspecific neighbours in territorial birds.

To test this hypothesis, we placed nest boxes in the forest in pairs in close proximity to one another, and as the nest boxes were occupied by great tits, we tested neighbouring individuals for neophobia. We also carried out experimental trials using a stuffed pine marten (*Martes martes*), a principal nest predator of small passerine birds in our study system (Krama and Krams 2005; Krams et al. 2007), to test for a relationship between the response to novel objects and the mobbing response to predators. Finally, we assessed whether these responses were related to later nest failure and survival of females during incubation. It has previously been shown that fledgling condition was affected by the interaction between male and female exploratory behaviour, with assortative pairs at both ends of the behavioural spectrum (i.e. 'bold-bold' pairs or 'shy-shy' pairs) producing fledglings in best condition (Both et al. 2005). Since boldness was expected to be an important determinant of nest defence, we predicted that pairs consisting of neophilic (bold) females and males would have the highest chances of nest survival, especially if their neighbouring pairs were neophilic (bold) individuals too. In contrast, the highest rates of nest failure were expected for pairs consisting of neophobic (shy) males and females, especially when breeding far from neighbours or when their neighbours were neophobic individuals too. We expected that neophilic individuals would defend their offspring more actively than neophobic individuals, by approaching predators closer, giving more alarm calls and performing longer mobbing activities in an attempt to move the predator away (Curio 1978; Pettifor 1990).

Methods

Study site and birds

The field study was carried out in June 2010, 2011 and 2012 near Krāslava, southeastern Latvia (54° 58' N, 27° 10' E; for more description of study site, see Rytkönen and Krams 2003). We placed nest boxes in pairs in pine forests of about 60 years of age containing a thick understory, and the distance between neighbouring nest boxes was either about 60 m (59.96 ± 1.71 m, mean $\pm$ SD) or about 350 m (358.80 ± 6.94 m, mean $\pm$ SD). Previous research showed that young coniferous forests represent a better breeding habitat than young deciduous forests for great tits in northern Europe: the birds have a better food availability and a higher number of fledglings per clutch in coniferous forests than in deciduous woods, fledglings are heavier in coniferous habitat and the rate of recruitment of fledglings is also higher in coniferous forests (Mänd et al. 2005; Mägi et al. 2009).

We had 40 pairs of nest boxes (80 nest boxes in total) in the distant neighbour group, and 38 pairs of nest boxes (76 nest boxes in total) in the close neighbour group. We monitored the onset of egg-laying phase to identify box pairs where the first eggs were laid either on the same day or the difference in the onset of egg laying did not exceed 2 days. This was done to ensure that nestlings are of the same age in the neighbouring nest boxes.

The identities of the most breeding birds were determined from colour plastic and metal leg rings. The age of the breeders that had not been ringed as nestlings was determined from plumage as first-year or older than 1 year (Svensson 1992) as soon as all of the trials were finished. We caught the birds by mist nets (Ecotone, <http://www.ecotone.pl>). Since some adults were not colour ringed before the trials, and colour rings often cannot be identified at the distance, all of the birds were then marked temporarily with non-toxic, acrylic paint, to identify which nest box they came from (Krams et al. 2008). The paint was applied to a piece of adhesive insulation foam placed inside the nest box entrance, so that the birds would mark themselves when entering and leaving the nest box. The paint lasted for 8–10 days. We inspected the nest boxes at least once a week to collect data on clutch and nestling success. This was done only when the females had left the nest boxes for short feeding bouts.

Novel object test

We tested a response of adults to a novel object when nestlings were about 8 days old (mean $\pm$ SD; 8.1 $\pm$ 1.5 days), and for a subset of subjects (10 nest boxes in the distant neighbour group and 11 nest boxes in the close neighbour group), we repeated the novel object test 2 days later when nestlings were about 10 days old (mean $\pm$ SD; 10.5 $\pm$ 1.7 days). We investigated individual variation in neophobia (risk responsiveness towards novel objects). We used a classic behavioural assay developed by Greenberg (1983) to assign ‘neophobia’ as the aversion to the unfamiliar, by the latency to return to known resources such as nest sites or feeders in the presence of a novel object (van Oers et al. 2004, 2005; Webster and Lefebvre 2000, 2001; Echeverria et al. 2006; Herborn et al. 2010). It is considered that the novel object generates a conflict between the desire to obtain the resource and the desire to avoid risks associated with the novel object (Richard et al. 2008). We used a purple tennis ball (diameter of 6.67 cm; Tourna Foam Tennis Practice Youth Balls) made of foam-rubber and placed on the top of nest box as a novel object, while repeated tests were performed by using a yellow tennis ball to prevent habituation. The ball was placed when, to the best of our knowledge, no great tit was nearby. We recorded the latency to resume nestling provisioning after the bird has detected the novel object for both the adult female and male of

each pair. The birds were observed from a distance of 50–60 m, and our presence did not affect bird behaviour.

Mobbing test

Nest defence in passerine birds usually takes the form of predator mobbing which is widespread among vertebrates (Pitcher et al. 1986; Krams et al. 2006b; Graw and Manser 2007). Joint predator mobbing in territorial neighbours has been observed in many passerine birds (Krams and Krama 2002; Krams et al. 2010, 2013; Krama et al. 2012b) including great tits (Grabowska-Zhang et al. 2012a). Mobbing trials were carried out when nestling age was between 12–16 days (mean $\pm$ SD=14.12 $\pm$ 1.10 days). This is a time when adults are predicted to invest more in older broods (Curio 1987). The stuffed pine marten was mounted on top of the nest box. It was installed when, to the best of our knowledge, no adult great tit was nearby. We removed the decoy as soon as the mobbing activities of nest owners stopped. The trial was repeated at the neighbouring nest at least 3 h later. All of the observations were done from a distance of 50–60 m. The order of the trials was chosen randomly by flipping a coin.

As soon as the pine marten model was discovered by one of the nest owners, we began documenting the mobbing response of the nest owners and their neighbours. We recorded the occurrence of joining of neighbouring individuals, the duration of mobbing activities, the minimum distance of approach and the number of alarm calls given by nest owners. While measuring the minimum distance from the predator, we evaluated the shortest distance of the focal bird to the predator during each trial. Before conducting the trials, we marked nearby tree trunks and branches, which allowed us to accurately measure the birds’ approach distances. We considered neighbours to have assisted the nest owners if they appeared in the vicinity of the nest (<15 m). We did not consider the neighbours to have assisted if they remained within their own territory—even if they interrupted their feeding activities and continuously gave alarm signals. An analysis of variance was performed for minimum approach distance, the number of alarm calls of resident birds and duration of mobbing in the close and distant groups. It was done to see if the group and the neighbours affect nest-defence behaviour of nest owners. By flipping a coin, we randomly chose 21 pairs of great tits to repeat the mobbing trials to test for repeatability of the minimum distance of approach 3 days later. All mobbing trials were performed blind with respect to the boldness of the birds to avoid observer bias.

Densities of heterospecific neighbours

Density of other nesting passerines was low at our study area. To evaluate the density of breeding birds, we counted all observed singing, foraging or resting within the radii of

100 m around each nest 4–6 days before the experimental trials (Krama et al. 2012a). We visited each site twice and the duration of each census was at least 20 min (26.36 ± 5.21 of mean census time, SD). The mean density of heterospecific passerine birds was similar between the sites of distant neighbour group (30.73 ± 4.25 pairs/km², mean $\pm$ SD) and close neighbour group (29.79 ± 4.70 pairs/km², mean $\pm$ SD). Thus, a possible dilution effect during the mobbing of predators can be treated as similar across all of the sites. It was recently shown that the number of heterospecific neighbours observed during the estimation of the density of local passerine birds corresponds to the number of birds observed during mobbing trials (Krama et al. 2012a). Although all of the neighbouring heterospecifics uttered alarm calls, none of them approached the predator closer than 10 m, and they never attacked the predator. Even the most active neighbouring heterospecifics finished their mobbing in a few minutes.

Statistics

The results of the novel object tests showed that the data were distributed in a bimodal way. Neophilic and neophobic responses were separated by using median split of the data obtained during the novel object test. We checked for overdispersion in the data by comparing the residual deviance to its degrees of freedom. Since this ratio was not greater than 1, we concluded that no overdispersion is present, which allowed us to use a generalised linear model (Gaussian error structure for duration and distance analyses and Poisson error and log link for the number of calls) for further analyses (Sokal and Rohlf 1995).

Ethical note

Some neophobic adult great tits interrupted food delivery to their nestlings for more than 1 h during the novel object test. The adults accelerated their feeding rate in the period immediately following the novel object test, and we did not observe any mortality of nestlings in these nests. A decrease in food delivery rate often can be observed during rain when feeding frequency drops to less than one per nestling per hour (Radford et al. 2001).

Results

Response latency to a novel object

The rates of response latency to resume feeding of nestlings measured from the moment the bird encountered the ball were not distributed normally (Kolmogorov-Smirnov test, $p < 0.001$). Instead, the birds appeared to fall under one of two ‘categories’ of the response latency. When great tits were

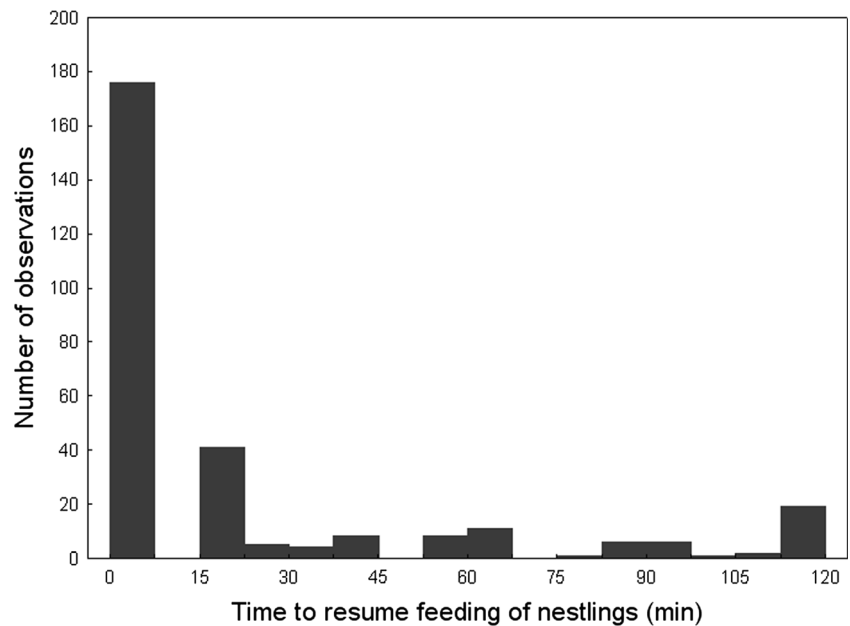
split into groups above and below the median response latency (median = 10.5 min), there was a significant difference between groups ($t = -16.42$, $df = 286$, $p < 0.001$; ‘neophilic response’, $n = 172$; 2.42 ± 1.69 min, mean $\pm$ SD; ‘neophobic response’, $n = 116$; 59.73 ± 38.74 min, mean $\pm$ SD) (Fig. 1). While neophilic great tits resumed feeding of nestlings within 0.10–5.20 min and neophobic birds resumed feeding activities within 16.10–122.80 min, we did not find any individual which resumed its nestling feeding within intermediate values of response latency between 5.20 and 16.10 min after finding a novel object on the top of its nest box (Fig. 1). When we tested these two groups separately for their data distributions, we found the rates of response latency were distributed normally (Kolmogorov-Smirnov tests; ‘neophilic response’, $p = 0.45$ and ‘neophobic response’, $p = 0.27$). Generalized linear model analysis showed significant differences between neophilic and neophobic individuals in their response latency to resume their nestling feeding ($F_{1,286} = 222.81$, $p = 0.0001$), while we did not find any significant difference between males and females ($F_{1,286} = 2.38$, $p = 0.12$), age groups ($F_{1,286} = 1.60$, $p = 0.21$), close and distant neighbour groups ($F_{1,286} = 2.01$, $p = 0.16$) and the years ($F_{1,286} = 1.04$, $p = 0.28$). The latency to resume feeding nestlings in response to purple and yellow balls as novel objects was highly repeatable ($R = 0.94$, $F_{20,21} = 32.28$, $p < 0.0001$).

Antipredator responses

All pairs of great tits arrived to mob the predator at their neighbours’ nests in the close neighbour group, while this was never observed in the distant neighbour distant neighbour group (Fisher’s exact test, $p < 0.0001$). The duration of mobbing response of nest owners varied between 4 and 900 s (416.42 ± 404.61 , mean $\pm$ SD), and it was significantly different among behavioural types of great tits (one-way ANOVA, $F_{2,285} = 225.30$, $p < 0.0001$).

Pairs consisting of neophilic-neophilic birds mobbed longer than pairs consisting of neophobic-neophobic (Tukey post-hoc test, $p < 0.001$) or neophilic-neophobic birds (Tukey post-hoc test, $p < 0.001$), and neophilic-neophobic pairs mobbed longer than neophobic-neophobic birds (Tukey post-hoc test, $p < 0.001$). Generalized linear model analysis showed that nest box proximity (close vs. distant pairs) ($F_{1,286} = 0.36$, $p = 0.56$, Table 1), sex ($F_{1,286} = 0.09$, $p = 0.77$), age ($F_{1,286} = 0.73$, $p = 0.40$) and the year ($F_{1,286} = 0.68$, $p = 0.43$) had no effect on duration of mobbing. The interaction between behavioural type and nest box proximity group was non-significant, showing that nest box proximity group and personality of focal birds had no effect on duration of mobbing (Table 1). However, the interaction between behavioural type of nest owners and behavioural type of their neighbours was significant, indicating that behavioural type of neighbours affected the duration of mobbing (Fig. 2a, Table 1).

Fig. 1 Latency to resume nestling provisioning from the first encountering the novel object



Neophobic-neophobic birds mobbed the predator longer when assisted by neophilic-neophilic neighbours (Tukey post-hoc, $p < 0.001$). However, they did not mob the predator longer when assisted by a mixed pair (Tukey post-hoc test, $p = 0.49$).

We found a significant heterogeneity in the minimum distance of approach to the predator ($0.01\text{--}25\text{ m}$, 6.97 ± 7.02 , mean $\pm$ SD) across behavioural types (one-way ANOVA, $F_{2,285} = 116.05$, $p = 0.0001$). Neophilic-neophilic pairs approached the predator significantly closer than pairs consisting of neophobic birds only (Tukey post-hoc test, $p < 0.001$), or pairs consisting of neophilic-neophobic individuals (Tukey post-hoc test, $p < 0.001$), whereas pairs consisting of neophilic-neophobic birds approached the predator closer than neophobic-neophobic pairs (Tukey post-hoc test, $p < 0.001$). Generalized linear model analysis showed that nest box proximity (close vs. distant pairs) ($F_{1,286} = 0.25$, $p = 0.46$, Table 1), sex ($F_{1,286} = 0.54$, $p = 0.47$), age ($F_{1,286} = 0.03$, $p = 0.87$) and the year ($F_{1,286} = 0.27$, $p = 0.60$) had no effect on the minimum distance of approach. The interaction between

behavioural type and nest box proximity group was non-significant, showing that nest box proximity group and personality of focal birds had no effect on the minimum distance of approach (Table 1). However, the interaction between behavioural type of nest owners and behavioural type of their neighbours was significant showing that behavioural type of neighbours affects minimum distance of approach of nest owners in the close neighbour group (Fig. 2b, Table 1). We found that neophobic-neophobic birds approached the predator closer when assisted by neophilic-neophilic pairs (Tukey post-hoc test, $p < 0.001$) or mixed pairs (Tukey post-hoc test, $p = 0.027$). The minimum distance of approach to the predator was highly repeatable ($r = 0.89$, $F_{20,21} = 18.62$, $p < 0.0001$).

We found a significant variance in the number of churring calls (Krams et al. 2006a) given by nest owners, which varied between 1 and 45 calls/min (17.33 ± 16.82 , mean $\pm$ SD) (ANOVA, $F_{2,288} = 469.46$, $p < 0.0001$). Pairs consisting of neophilic individuals gave significantly more calls than pairs consisting of neophobic birds (Tukey post-hoc test, $p < 0.001$)

Table 1 The effects of behavioural types (personality) of nest owners, behavioural types (personality) of their neighbours and the group (close vs. distant pairs) on duration of nest defence, the minimum approach

distance to the predator and the number of calls given during mobbing of the predator (Generalized linear model analysis)

	Duration of mobbing				Minimum distance of approach				Number of calls			
	df	MS	F	p	df	MS	F	p	df	MS	F	p
Personality	2	622.25	149.36	0.001	2	193.74	205.40	0.0001	2	5627.7	275.56	0.0001
Neighbour personality	2	59.67	14.32	0.001	2	41.16	43.63	0.0001	2	184.73	9.05	0.0001
Group	1	0.31	0.36	0.56	1	0.23	0.25	0.46	1	0.15	0.24	0.87
Personality $\times$ group	1	0.20	0.38	0.48	1	0.45	0.51	0.32	1	0.27	0.39	0.46
Personality $\times$ neighbour	3	79.07	18.98	0.001	3	78.56	83.29	0.0001	3	398.67	19.52	0.001
Personality												

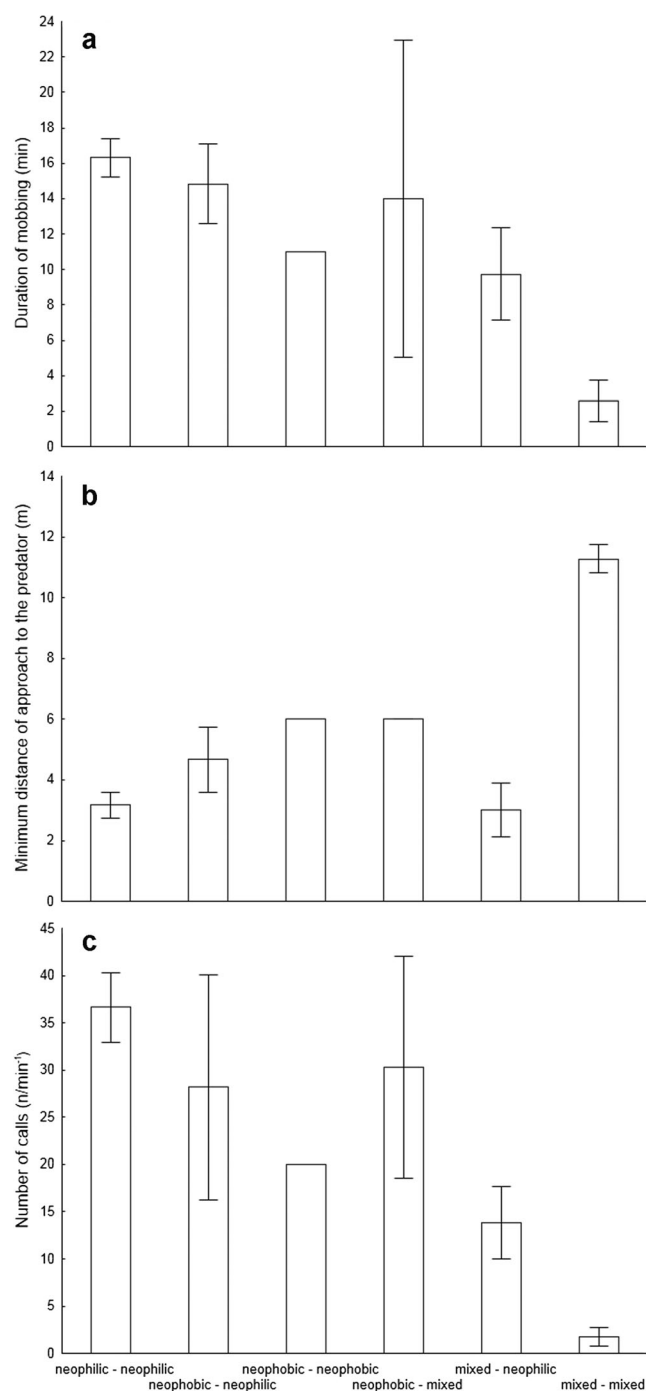


Fig. 2 Interactions of nest owner personality and their neighbour personality in close neighbour group for the duration of mobbing, minimum distance of approach to the predator and the number of mobbing calls given (means and standard errors). Each combination shown consists of response type to a novel object of nest owners followed by response type of neighboring pair (e.g. neophilic-neophilic)

and those consisting of neophobic and neophilic individuals (Tukey post-hoc test, $p < 0.001$), while mixed pairs uttered more calls than pairs of neophobic-neophobic birds (Tukey post-hoc test, $p < 0.001$). Generalized linear model analysis revealed that the number of calls did not differ between nest

box proximity groups ($F_{1,286} = 0.24$, $p = 0.87$, Table 1), sex groups ($F_{1,286} = 3.10$, $p = 0.08$), age groups ($F_{1,286} = 0.01$, $p = 0.93$) and the years ($F_{1,286} = 2.21$, $p = 0.11$). The interaction between behavioural type and nest box proximity group was non-significant, showing that nest box proximity group and personality of focal birds had no effect on the number of calls. However, it was significantly affected by behavioural type of nest owners and behavioural type of their neighbours (Fig. 2c, Table 1). It was found that neophobic-neophobic birds gave more calls when assisted by neophilic-neophilic pairs (Tukey post-hoc test, $p < 0.0001$), while neophobic-neophobic birds did not call more when assisted by mixed pairs ($p = 0.80$).

The total duration of mobbing was positively correlated with the number of alarm calls/min ($r = 0.85$, $n = 288$, $p < 0.001$) and was negatively correlated with the minimum distance of approach ($r = -0.83$, $n = 288$, $p < 0.001$). The minimum distance of approach was negatively correlated with the number of alarm calls given ($r = -0.81$, $n = 288$, $p < 0.0001$) suggesting that more calls are given in the proximity of predators.

Surprisingly, some nest owners attacked their assisting neighbours, and we observed that neighbours were sometimes chased up to 20–25 m away from the nest box, just when the stuffed marten was placed on the top of their nest boxes. The incidence of attacks towards neighbouring pairs was significantly higher among neophilic-neophilic ($n = 10$ out of 38) than in neophobic-neophobic ($n = 1$ out of 28) pairs of nest owners ($\chi^2 = 4.48$, $df = 1$, $p = 0.034$) in the close neighbour group.

Nest failure

In total 24 out of 80 nests of great tits were depredated in the distant neighbour group, while only 10 out of 76 nests failed due to predation in the close neighbour group across incubation and nestling phase revealing that nest predation rate was significantly higher in breeders of the distant neighbour group ($\chi^2 = 5.54$, $df = 1$, $p = 0.02$). In the distant neighbour group, 9 out of 24 nests were depredated during the incubation period, and all nine females were killed within their nest boxes. In the close neighbour group, 3 out of 10 nests were depredated during the incubation period, and only one female was killed, showing that the survival of incubation females is significantly higher in the close neighbour group ($\chi^2 = 7.26$, $df = 1$, $p = 0.007$). No nest predation was detected in either nest box proximity group between hatching and until nestlings reached the age of 10 days.

We tested females and males whose nests survived until the nestlings fledged or that were depredated during the nestling phase. In the close neighbour group, we found that 38 out of 73 pairs consisted of neophilic males and neophilic females, 28 pairs consisted of neophobic males and neophobic females, and only 7 pairs were mixed (one mate neophilic, the other one neophobic). In the distant neighbour group, 41 out of 71

pairs were composed of neophilic males and neophilic females, 23 pairs were composed of neophobic males and neophobic females, and 7 pairs consisted of mixed partners. In the close neighbour group, 3 out of 7 failed pairs consisted of neophobic females and neophobic males, and 4 pairs consisted of neophilic males and neophilic females. In the distant neighbour group, 1 out of 15 failed nests belonged to neophilic-neophilic pairs, 1 nest to neophilic-neophobic pair and 13 nests belonged to neophobic-neophobic pairs. Thus, the proportion of pairs consisting of only neophilic or only neophobic individuals was the same in the close and distant neighbour groups ($\chi^2=0.33$, $df=1$; $p=0.56$), but nests of neophobic birds had higher chances of nest failure than nests of neophilic individuals or nests of mixed pairs in the distant neighbour group (a 3×2 contingency table: $\chi^2=20.57$, $df=2$; $p=0.0001$; Fig. 3). The chance of nest survival of neophobic-neophobic pairs was higher when birds of this behavioural type were breeding in the close neighbour group ($\chi^2=10.27$, $df=1$; $p=0.001$), whereas nest survival was the same between the nest box proximity groups for pairs consisting of neophilic-neophilic great tits ($\chi^2=1.025$, $df=1$; $p=0.31$) (Fig. 3).

In 25 cases of nest failure, nests were most likely depredated by pine martens, because the top of the nest boxes had been removed. In another nine cases, the nests were depredated by smaller mammalian predators such as the stoat (*Mustela erminea*) or weasel (*Mustela nivalis*).

Discussion

The main finding of this study is that consistent individual differences in response to novel objects and

antipredator behaviour are related to each other. Furthermore, these responses are important predictors of nest failure in great tits. We found that neophilic individuals have an advantage over neophobic individuals in their reproductive success, as measured in numbers of success nests and survived females. In great tits, individual corticosterone responses derived from a handling trial predict neophobia (Groothuis and Carere 2005). Likewise, exposure to predators may cause a stress response and elicits a release of corticosterone (Tilgar et al. 2011), suggesting similar physiological mechanisms may underlie the responses to novel objects and predators.

Nest defence behaviour is important in driving predators away (Flasskamp 1994; Curio and Regelmann 1985, 1986; Pettifor 1990). Mobbing and predator attacks are a rapid event and requires immediate and well-coordinated activities by prey individuals. As pointed out by Krebs (1978), aggressive individuals should have an advantage over more docile individuals. Our results are in agreement with this suggestion, since shy and neophobic individuals should have little chance to protect their nest against an approaching predator, whereas neophilic and bold individuals could affect the predator during the earliest phase of the attack. Neophilic great tits do this by approaching the predator closer than neophobic individuals and giving more calls, perhaps to signal to the predator that it has been spotted and that it has no any chance for the attack based on surprise (Krams and Krama 2002; Krams et al. 2013).

No experimental study has shown so far that neophilic and more active mobbers can deter an attack by predators with a higher probability than neophobic and shy mobbers. However, non-experimental evidence is increasingly suggesting that active and exaggerated mobbing provides a better protection for offspring (Curio 1978; Flasskamp 1994; Grabowska-Zhang et al. 2012a). It is also important to note that it was easy to discriminate between neophilic and neophobic individuals during the novel object test, and that both the novel object test and the mobbing test showed that resuming feeding of nestlings and nest-defence behaviour requires bold behaviour under conditions of high predation risk.

Dilution of predation risk is one of the most important benefits of being a group member (Krause and Ruxton 2002). The results of this study also show that nest survival is dependent not only on personality-like behavioural type of breeding birds, but also on the proximity to conspecific neighbours. The pairs composed of neophobic mates had significantly higher rates of nest failure than pairs consisting of mixed or neophilic individuals in the distant neighbour group due to predation. The neophobic pairs significantly improved

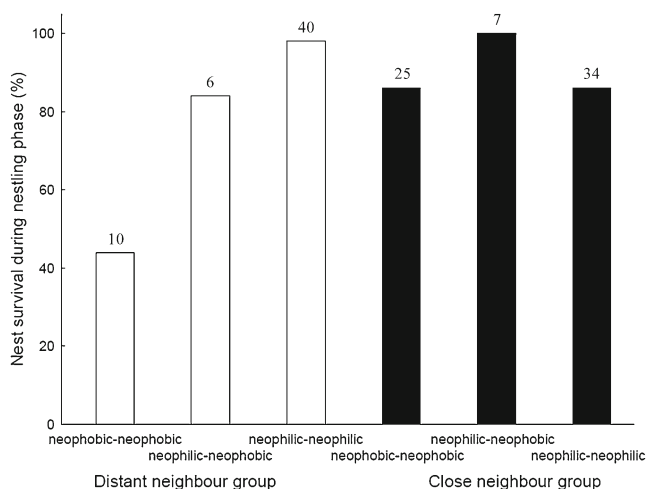


Fig. 3 Nest survival during provisioning stage and its dependence on the nest box proximity group and behavioural type of their neighbours (number of survived nests)

their reproductive success by joining other conspecifics in the close neighbour group, whereas neophilic pairs had the same rate of nest failure across the groups. These results suggest a protective effect by conspecific neighbours for neophobic or less active individuals. This, therefore, shows that the social environment is important to territorial species that are generally considered to have limited social interactions (Grabowska-Zhang et al. 2012a, b; Freeberg et al. 2012; Krams et al. 2012). Stable relationships with territorial neighbours may lead to reduced aggression in territory defence (Briefer et al. 2008; Brunton et al. 2008; Rosell et al. 2008), and repeated interactions with the same individuals aid the evolution of cooperation (Krams et al. 2008).

Recent studies by Grabowska-Zhang et al. (2012a, b) revealed positive effects of increased familiarity among breeding pairs of great tits: breeders with more familiar individuals in their neighbourhood laid larger clutches and had a greater chance of successfully fledging offspring. Familiarity with neighbours may provide public information about the availability of potential mates and potential nearby territories (Bergmüller et al. 2005), and may improve antipredator protection (Kokko and Ekman 2002). Further, it has been shown that neighbours in some territorial species may benefit by cooperation to drive their nest predators away (Milinski 1987; Olendorf et al. 2004; Wheatcroft and Krams 2009; Krams et al. 2006a, 2008). However, this study shows that benefits of having neighbours can be asymmetrical for the involved parties and may in part be influenced by behavioural type of the individuals. First of all, only neophobic individuals benefit from having neophilic individuals as neighbours, while this was not true for neophilic birds. Second, neophilic individuals provide not only protection for incubating females and increased protection of offspring in the neighbourhood, but they also direct their aggressiveness towards their neighbours during nest defence events. Perhaps, the increased aggressiveness of neophilic great tits should be tolerated by neophobic individuals only under conditions of high predation risk, whereas it would be more beneficial to stay away from neophilic individuals under conditions of low predation risk.

In this study, the personality was determined in a neophobia test, and we found that neophilic individuals explored the novel object from close distances and did so rapidly, whereas neophobic birds explored the object from greater distances and took more time to explore. Mobbing tests also helped to reveal boldness of individual great tits, and these tests were especially useful when applied together. We found that duration of mobbing and the number of churring calls given to the pine marten model negatively correlated with the latency to resume feeding in the novel object test. The minimum distances of approach to the stuffed predator were positively correlated with the response latency to resume feeding behaviour in the novel object test. Thus, neophilic individuals mobbed more intensively and approached the predator closer

during mobbing tests. However, the emission of mobbing signals and close proximity to the predator puts the mobber in jeopardy (e.g. Curio 1978), and future research should find out as to how bold individuals avoid the risk of being attack.

Our results support the previous studies showing that social interactions can affect fitness of individuals that are territorial during the breeding season (Grabowska-Zhang et al. 2012a, b). We found that fitness may differ according to the type of response to the unfamiliar object and nest predator, and that these responses are dependent on individual personality. Our results reveal that neophilic individuals returned to feeding of their nestlings sooner than neophobic individuals from the moment they encountered the novel object, and the intensity of nest defence was more intense in neophilic great tits. Finally, we show that strength of antipredator responses of breeding great tits may also depend on personality type of neighbouring conspecifics. Future work is needed to address the underlying mechanisms of how cooperation among neighbours influences individual fitness.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All animal manipulations reported therein comply with the current laws in Latvia.

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